

The use of Taylor's Power Law to describe the aggregated distribution of earthworms in permanent pasture and arable soil in Scotland

B. Boag¹, R. K. Legg², R. Neilson¹, L. F. Palmer¹ and C. A. Hackett³

¹ Zoology Department, Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, Scotland, UK

² University of East London, Romford Road, London E15 4LZ, England, UK

³ Scottish Agricultural Statistics Service, Invergowrie, Dundee DD2 5DA, Scotland, UK

Summary. The aggregated horizontal distribution of earthworms was investigated in 200 fields on 100 farms throughout Scotland using Taylor's power law. Results indicated that the index of aggregation b was relatively consistent for juvenile and adult earthworms from both pasture and arable fields. It is suggested that before statistical analysis the most appropriate transformation for these populations would be a $\sqrt[3]{\cdot}$ transformation.

Key words: Taylor's Power Law, aggregation, transformation, earthworms

Introduction

Earthworms are known to have an aggregated distribution in the soil and as a necessary pre-requisite to the development of efficient sampling techniques and population studies detailed investigations have been undertaken into the vertical distribution of a number of species (Gerard 1967; Persson & Lohm 1977; Reinecke & Viljoen 1990). Less is known about the horizontal aggregated distribution of earthworms (Stein et al. 1992) or the necessity to transform the data before statistical analysis. McCredie et al. (1992) used $\sqrt{x + 0.5}$ to normalise their data while Ma et al. (1990) and Potter et al. (1990) both used $\log(x + 1)$ transformations. Daniel et al. (1992) found data on *Lumbricus terrestris* L. could be described by a Poisson distribution but had to use a negative binomial distribution for juveniles. However the negative binomial distribution has been criticised by Taylor et al. (1979) who showed that over a wide range of densities the aggregation parameter k could vary with density in a way that was non-linear. They preferred to summarise aggregated data using Taylor's variance-mean model (Taylor 1961) which expresses the variance, V , as a power of the mean, μ , of the distribution:

$$V = \alpha\mu^b \quad (1)$$

This power law (1) does not describe a probability distribution but a relationship between the variance and mean of a distribution. Taylor's power law can also be used to determine the transformation required to stabilise the population variance before carrying out an analysis of variance. The transformation is:

$$z = x^{1-b/2}$$

Correspondence to: Brian Boag

where x denotes an observation whose probability distribution satisfies Taylor's power law (Taylor 1970; Finch et al. 1975).

Although the aggregation of a wide range of organisms has been investigated using Taylor's power law (Taylor et al. 1978; Boag & Topham 1985) only two earthworm species, *Allolobophora chlorotica* (Savigny) and *Aporrectodea caliginosa* (Savigny), have previously been studied using the data from Gerard (1960).

The purpose of the present paper is to use Taylor's power law to study the aggregation of both adult and juvenile earthworms from arable and pasture fields in Scotland and to investigate their optimum variance stabilising transformation.

Materials and Methods

A stratified random sample of 100 arable farms in Scotland was produced by the Scottish Office for a survey to detect the presence of *Artioposthia triangulata* (Dendy), a predatory planarian, which feeds on earthworms and has been shown to have a widespread distribution in Ireland and Scotland (Blackshaw 1989; Boag et al. 1993). At each farm between 10.00 a.m. and 4.00 p.m. two fields were chosen (where possible one arable and one permanent pasture) and, in a randomly selected area of the field, five 0.25 m² metal square quadrants were sunk 5–10 cm into the ground at 10 m intervals from each other. The 10 m interval was chosen as the minimum distance between sampling points where it was considered earthworm counts would probably be independent of one another. Grass and any other vegetation was cut to ground level and removed. Although the efficiency of the formaldehyde method for extraction of worms is known to vary with species, season and time it has been used as the standard technique by many authors (Daniel et al. 1992) and for that reason was chosen for the present survey. Two applications of 0.5% formaldehyde solution (4.5 litres per application) were evenly applied within each quadrant. The second application was applied once earthworms had ceased emerging after the first application (Blackshaw 1990). At each stage any earthworms that emerged were collected and preserved in 4% formaldehyde for identification at a later date. The means and variances used in this paper were taken from the earthworm counts from the five quadrats from each field.

The data from the individual species were combined to (a) reduce the number of samples with zero values which if they were too numerous could bias the estimation of the index of aggregation, and (b) cause the data to be of more general use, since very few earthworm communities are composed of only one species.

The Taylor's power law index of aggregation was estimated by b , the slope of the regression line of $\log(\text{sample variance} + 0.001)$ on $\log(\text{sample mean} + 0.001)$ and the upper bound b' was estimated according to Perry (1981). Calculations were undertaken using the statistical program Genstat 5 release 2.2 (Payne et al. 1987).

Result

The estimated values of Taylor's power law index of aggregation for adult and juvenile earthworms in arable and pasture fields can be seen in Table 1. The results indicate that the amount of aggregation was relatively low, the overall b value being 1.35. The adult worms had lower b values in both arable and pasture fields than juveniles, but the differences were not significant, and overall the amount of aggregation appeared relatively consistent irrespective of the field crop or earthworm development stage. The regressions accounted for 65–85% of the variation. The 'a' value, which has been considered a sampling factor (McSorley et al. 1985), was low but had a positive value for all the categories. The standard error associated with 'a' was relatively consistent especially between both juveniles and adults and arable and pasture fields.

The index of aggregation of 1.35 corresponds to a variance-stabilising transformation $z = x^{0.325}$, close to a cube root transformation. The normality of the transformed residuals after analysis of variance was investigated for the following transformations: untrans-

Table 1. Estimates of Taylor's power law index of aggregation b for earthworm populations in arable and pasture fields in Scotland

	n	b value	Standard error	b' value* a	Standard error	Percentage variance accounted for by the regression of log (va- riance ± 0.001) on log (mean ± 0.001)
Arable						
Adults	68	1.19	0.10	1.60	0.16	73.6
Juveniles	68	1.32	0.07	1.55	0.35	84.9
Total No.	68	1.38	0.07	1.60	0.24	85.6
Pasture						
Adults	132	1.27	0.08	1.94	0.11	65.0
Juveniles	132	1.31	0.06	1.64	0.41	79.5
Total No.	132	1.33	0.07	1.76	0.38	75.2
Arable & Pasture						
Adults	200	1.24	0.06	1.78	0.14	69.5
Juveniles	200	1.31	0.05	1.59	0.38	82.3
Total No.	200	1.35	0.05	1.67	0.31	80.9

* b' is the upper bound on the true value of the index of aggregation (Perry, 1981)

formed, square root, cube root, $X^{0.325}$ and log, using the probability plot correlation test (Filliben 1975). The correlation of the cube root, the square root and the $X^{0.325}$ transformation suggested by Taylor's power law were high (0.998, 0.995, 0.998 respectively) but those for the untransformed or log transformed data were lower suggesting these did not normalize the data adequately.

Discussion

The survey detected 13 species of earthworms, the most prevalent being *Aporrectodea caliginosa*, *A. longa* (Ude) and *Lumbricus terrestris*. All species had a widespread distribution except for *L. festivus* (Savigny) which was mainly restricted to the south and west of Scotland (unpublished data). The only previous use of Taylor's power law was restricted to *Allobophora chlorotica* and *Aporrectodea caliginosa* where the indices of aggregation b were found to be 1.59 ± 0.16 and 1.62 ± 0.35 respectively (Taylor et al. 1978). These results are greater than those recorded during the present investigation using mixed earthworm populations where the overall b value was found to be 1.35 ± 0.05 . The reason for this is unclear but could be explained by possible interspecific competition between species displacing some species so that a more even distribution of total earthworm populations becomes apparent. The b value did not differ markedly between adults and larvae as reported by Daniel et al. (1992) who found juvenile stages to have a more aggregated distribution than adults.

A b value of 1.35 suggests that a cube root transformation would normalise the data. A square root transformation was also found to normalise the data but the log transformation did not. However the above recommendations have been derived from only 100 arable farms and it would be prudent for other investigators to derive their own index of aggregation since a difference in the species composition of an earthworm fauna might alter the b value (Taylor et al. 1988). For this reason any future work would also benefit from the identification and analysis being done at species level.

Acknowledgements

This work was carried out as part of a Flexible Funded Project financed by the Scottish Office Agriculture and Fisheries Department. We gratefully acknowledge the help given by Dr. S. Chambers, National Museums of Scotland, Edinburgh and the consent of all the farmers who allowed us access to their land.

References

- Blackshaw, R. P. (1989) The effects of a calcareous seaweed product on earthworms in a grassland soil. *Biol. Ag. Hort* **6**, 27–33.
- Blackshaw, R. P. (1990) Studies on *Artioposthia triangulata* (Dendy) (Tricladida: Terricola), a predator of earthworms. *Ann. appl. Biol.* **116**, 169–176.
- Boag, B., Topham, P. B. (1985) Aggregation of plant parasitic nematodes and Taylor's power law. *Nematologica* **30**, 348–357.
- Boag, B., Yeates, G. W., Johns, P. M., Neilson, R., Palmer, L. F. & R. K. Legg (1993) Distribution of the New Zealand flatworm (*Artioposthia triangulata*) in New Zealand and Scotland. *Acta Zool. Fenn.* (in press).
- Daniel, O., Jager, P., Cuendet, G. & M. Bieri (1992) Sampling of *Lumbricus terrestris* (Oligochaeta, Lumbricidae). *Pedobiologia* **36**, 213–220.
- Filliben, J. R. (1975) The probability plot correlation coefficient test for normality. *Technometrics* **17**, 111–117.
- Finch, S., Skinner, G. & G. H. Freeman (1975) The distribution and analysis of cabbage rootfly egg populations. *Ann. appl. Biol.* **79**, 1–18.
- Gerard, B. M. (1960) The biology of certain British earthworms in relation to environmental conditions. Unpublished PhD thesis, University of London.
- Gerard, B. M. (1967) Factors affecting earthworms in pasture. *J. Anim. Ecol.* **36**, 235–252.
- Ma, W. C., Brussaard, L. & J. A. Deridder (1990) Long term effects of nitrogenous fertilizers on grassland earthworms (Oligochaeta: Lumbricidae): Their relation to soil acidification. *Agric. Ecosyst. Environ.* **30**, 71–80.
- McCredie, T. A., Parker, C. A. & I. Abbott (1992) Population dynamics of the earthworm *Aporrectodea trapezoides* (Annelida: Lumbricidae) in a Western Australian pasture. *Biol. Fertil. Soils* **12**, 285–289.
- McSorley, R., Dankers, W. H., Parrado, J. L. & J. S. Reynolds (1985) Spatial distribution of the nematode community of Perrine Marl soils. *Nematropica* **15**, 77–92.
- Payne, R. W., Lane, P. W., Ainsky, A. E., Bicknell, K. E., Digby, P. G. N., Harding, S. A., Leech, P. K., Simpson, H. R., Todd, A. D., Verrier, P. J. & R. P. White (1987) *Genstat 5 reference manual*. Clarendon Press, Oxford. pp. 1–749.
- Perry, J. N. (1981) Taylor's power law for dependence of variance on mean in animal populations. *App. Stats.* **30**, 254–263.
- Persson, T. & U. Lohm (1977) Energetical significance of the annelids and arthropods in a Swedish grassland soil. *Ecol. Bull. (Stockholm)* **23**, 1–211.
- Potter, D. A., Buxton, M. C., Redmond, C. T., Patterson, C. G. & A. J. Powell (1990) Toxicity of pesticides on earthworms (Oligochaeta: Lumbricidae) and effect on thatch degradation in Kentucky bluegrass turf. *J. Econ. Ent.* **83**, 2362–2369.
- Reinecke, A. J. & S. A. Viljoen (1990) The influence of worm density on growth and cocoon production of the compost worm *Eisenia fetida* (Oligochaeta). *Rev. Ecol. Biol. Sol.* **11**, 27, 1–10.
- Stein, A., Bekker, R. M., Blom, J. H. C. & H. Rogaar (1992) Spatial variability of earthworm populations in a permanent polder grassland. *Biol. Fertil. Soils* **14**, 260–266.
- Taylor, L. R. (1961) Aggregation, variance and the mean. *Nature (London)* **189**, 732–735.
- Taylor, L. R. (1970) Aggregation and the counts of *Aphis fabae* Scop. on beans. *Ann. appl. Biol.* **65**, 181–189.
- Taylor, L. R., Perry, J. N., Woivod, I. P. & A. J. Taylor (1988) Specificity of the spatial power law exponent in ecology and agriculture. *Nature* **332**, 721–722.
- Taylor, L. R., Woivod, I. P. & J. N. Perry (1978) The density-dependence of spatial behaviour and the rarity of randomness. *J. Anim. Ecol.* **47**, 383–406.
- Taylor, L. R., Woivod, I. P. & J. N. Perry (1979) The negative binomial as a dynamic ecological model and the density dependence of *k*. *J. Anim. Ecol.* **48**, 289–304.
- Taylor, L. R., Woivod, I. P. & J. N. Perry (1980) Variance and the large scale spatial stability of aphids, moths and birds. *J. Anim. Ecol.* **49**, 831–854.